Differences in recovery between deep-sea hydrothermal vent and vent-proximate communities after a volcanic eruption

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All authors contributed to writing of the manuscript and approved the final article.

SG and MB were responsible for project development, analyses of data and writing of the manuscript. SG identified meiofauna and macrofauna; BG identified macrofauna; PMA identified meiofauna; SM performed water column sampling; NLB measured and analysed abiotic variables; MW analysed prokaryote abundances; TMS provided 3 month-long deployed benthic control samples;

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Abstract

Deep-sea hydrothermal vents and the surrounding basalt seafloor are subject to major natural disturbance events such as volcanic eruptions. In the near future, anthropogenic disturbance in the form of deep-sea mining could also significantly affect the faunal communities of hydrothermal vents. In this study, we monitor and compare the recovery of insular, highly productive vent communities and vent-proximate basalt communities following a volcanic eruption that destroyed almost all existing communities at the East Pacific Rise, 9°50'N in 2006. To study the recovery patterns of the benthic communities, we placed settlement substrates at vent sites and their proximate basalt areas and measured the prokaryotic abundance and compared the meio- and macrofaunal species richness and composition at one, two and four years after the eruption. In addition, we collected samples from the overlying water column with a pelagic pump, at one and two years after the volcanic eruption, to determine the abundance of potential meiofauna colonisers. One year after eruption, mean meio- and macrofaunal abundances were not significantly different from pre-eruption values in vent habitats (meio: 8 - 1838 ind. 64 cm⁻² in 2006; 3 - 6246 ind. 64 cm⁻² in 2001/02; macro: 95 - 1600 ind. 64 cm⁻² in 2006; 205 - 4577 ind. 64 cm⁻² in 2001/02) and on non-vent basalt habitats (meio: 10 - 1922 ind. 64 cm⁻² in 2006; 8 - 328 ind. 64 cm⁻² in 2003/04; macro: 14 - 3351 ind. 64 cm⁻² in 2006; 2 - 63 ind. 64 cm⁻² in 2003/04), but species recovery patterns differed between the two habitat types. In the vent habitat, the initial community recovery was relatively quick but incomplete four years after eruption, which may be due to the good dispersal capabilities of vent endemic macrofauna and vent endemic dirivultid copepods. At vents, 42 % of the pre-eruption meio- and 39 % of macrofaunal species had returned. In addition, some new species not evident prior to the eruption were found. At the tubeworm site Tica, a total of 26 meio- and 19 macrofaunal species were found in 2009, which contrasts with the 24 meio- and 29 macrofauna species detected at the site in 2001/02. In the basalt habitat, community recovery of meiofauna was slower with only 28 % of the original 64 species present four years after eruption. The more limited dispersal capabilities of meiofauna basalt specialists such as nematodes or harpacticoid copepods probably caused this pattern. In contrast, 67 % of the original 27 macrofaunal species had recolonized the basalt by 2009. Our results suggest that not only vent communities, but also species-rich communities of vent-proximate habitats require attention in conservation efforts.

1.Introduction

All organisms living at deep-sea hydrothermal vents and on vent-proximate basalt are subject to natural disturbances, i.e. volcanic eruptions. On fast spreading ridges like the 9°50'N East Pacific Rise (EPR), eruptions occur frequently, with time intervals of only 15 years, and vent sites are typically separated by a few kilometers (Haymon et al., 1991; Shank et al., 1998; Tolstoy et al., 2006). In contrast, vent sites on slow spreading centers are more distant from each other and major disturbance events occur less frequently (German et al., 1996; Humphris et al., 2002; Murton et al., 1994). Organisms occur in a wide range of environmental conditions, and it is crucial to consider dispersal and connectivity patterns of meio- and macrofauna in order to address recovery mechanisms in response to disturbance and productivity regimes. Vent animals live in highly dynamic environments, with intermittent exposure to temperature peaks, substantial concentrations of hydrogen sulfide, variable heavy metal exposure, and reduced oxygen availability, but high in situ primary production. Megafauna, such as tubeworms or mussels, act as foundation species and provide a habitat for the associated macro- and meiofauna (Fisher et al., 2007; Van Dover, 2000). The endemism, abundance, and biomass of vent macrofaunal communities is much higher, but diversity is much lower than sedimented deep-sea habitats at similar depths (Moalic et al., 2012; Tunnicliffe, 1992). Macrofaunal dispersal between isolated vent sites occurs primarily in the larval stage, but demersal, dispersal and migration can also occur (Mullineaux et al., 2010, 2005). In general, meiofauna are similarly diverse to macrofauna, but are not exceptionally abundant, and many vent meiofaunal species are not restricted to vents, but also occur on proximate basalt (Gollner et al., 2010b, 2007). The dispersal mechanisms of vent meiofauna have not been studied yet.

On basaltic rock proximate to vents under ambient deep-sea conditions, low temperatures are stable and *in situ* primary production is negligible. The source of nutrition is suspended photosynthetic-derived material from surface waters and particulate organic matter originating from the nearby active vents (Erickson et al., 2009; Levin et al., 2009). Dominant macrofauna include sparsely distributed sponges, hydroids, anemones, squat lobsters, ophiuroids, and holothurians (Galkin, 1997). In addition, vent-associated macrofaunal taxa were found on proximate basalt, although in low abundance and low biomass (Gollner et al., 2015; Marcus and Tunnicliffe, 2002). At 9°50'N East Pacific Rise, a species-rich but low abundance meiofaunal community was documented on vent-proximate basalt (Gollner et al., 2010b). Dispersal and biogeography of basalt species are almost unknown, but a

macrofaunal study showed unexpectedly high levels of genetic differentiation for squat lobsters (Thaler et al., 2014)..

The East Pacific Rise, like other mid ocean ridges, has rich deposits of metals in the form of massive sulfide deposits (SMS). Currently, various regions along the Mid Atlantic Ridge and the Indian Ocean Triple Junction are being explored for mining (SPC, 2013). Exploitation of sulfide minerals is expected to disturb communities living at hydrothermal vents and in surrounding areas (Van Dover, 2011). The first deep-sea massive sulfide mine could open in Papua New Guinea as soon as 2016 (Gramling, 2014). However, the scale of environmental impacts remains to be determined, and there are many unknowns in the ecology and connectivity of populations at active and inactive SMS deposits (Boschen et al., 2013; Van Dover, 2011). Recommendations to evaluate the possible impact of mining (disturbance) include identification of conservation areas, as well as determination of natural conservation units for key species with different size and life histories and dispersal strategies (Van Dover, 2011). Different life-histories of meio- and macrofauna include for example mode of development (direct benthic versus planktonik), dispersal (as adults versus as larvae), generation time (less than one year versus more than one year), or potential number of off-spring (small versus large) (Warwick 1984). Within the meiofauna, nematodes show less dispersal potential than copepods (Giere 2009). The effect of disturbance on the vent-proximate basalt areas has received relatively less attention than vent habitats, although future mining operations will probably mostly impact the vent-surroundings with their mining-machines. Volcanic eruptions naturally disturb hydrothermal vents and the vent-proximate areas; understanding these recovery mechanisms will help to formulate plans for future conservation.

The recent volcanic eruption at the 9°50'N EPR in 2005/2006 covered an area of several km² with lava (Tolstoy et al. 2006) (see Figure 1) and provided the opportunity to examine colonization and recovery patterns of meio- and macrofauna in hydrothermal vent and ambient basalt habitats. In particular, we consider the influence of species-specific traits such as dispersal ability and contrast patchy (active vent) and continuous habitat areas (ambient bare basalt). We hypothesize that vent-restricted species have high dispersal potential and therefore relatively rapid recovery rates after disturbance, whilst species in the continuous non-vent basalt habitat might have less potential to disperse over wider distances and thus could delay recovery. In addition, the general high abundances of single species at vents (e.g. Fisher et al., 2007) could enhance recovery, whilst the general low

abundances of standing populations (and thus gametes) of single species on basalt (Gollner et al., 2015, 2010b) could slow down recovery. Further, we hypothesize that life-history traits of meio- and macrofauna influence recolonization. We infer that macrofauna have high dispersal potential and can quickly colonize the disturbed area. Within the meiofauna we expect that copepods show greater dispersal and thus faster colonization than nematodes. A study on nematode recovery after the eruption at the 9°50'N EPR already showed that nematodes apparently required a relatively long time to colonize the lava-flooded area (vent and basalt) in greater numbers and richness (Gollner et al., 2013).

To study recovery patterns in the benthic community, we placed settlement substrates at recently established vent tubeworm sites and their proximate basalt areas. We examined meio- and macrofaunal abundances, species richness and composition at one, two and four years after the eruption. To study potential food-limitation after eruption (bottom-up control), prokaryote abundances were analyzed one year after eruption at vents and on basalt. Abundances of newly assembled meio- and macrofaunal communities after the eruption were also compared to benthic communities sampled prior to the eruption in 2001-2004 (Gollner et al., 2015, 2010b). To determine the influence of dispersal on benthic community recovery, macrofaunal larvae (Mullineaux et al., 2010) and meiofauna were collected with pelagic pumps one and two years after eruption.

2. Material and methods

2.1. Benthic collections

To obtain quantitative meio- and macrofaunal species abundances, three settlement substrates each were recovered at the vent sites Tica, Sketchy, and P-Vent, and three settlement substrates on proximate bare basalt areas. They were all located at ~2500 meters depth in the 9°50'N region of the East Pacific Rise (EPR) and were studied over four years, in December 2006, November 2007 and December 2009 (Table 1, Figure 1, 2). Each settlement substrate used at vent habitats consisted of 2 plastic kitchen sponges with a circular surface area of ~64 cm². Each settlement substrate used on basalt consisted of 4 plastic kitchen sponges in order to enhance sample size (Figure 2). Settlement substrates were deployed and recovered with the submersible *Alvin*.

To test suitability of sponges as settlement substrates, we recovered natural *in situ* community samples from basalt and vent habitats. Natural community samples were taken with the arm of *Alvin* by grabbing a piece of rock (devoid of megafauna at basalt habitat; with foundation species at vent habitat). Each sample

was placed into an isolated box on the platform of *Alvin*. To allow a comparison with settlement devices, we estimated surface area by covering the sampled rock with aluminum foil, photographing it and calculating its area with the AnalySIS program. We found no significant differences in abundance, species richness, expected number of species after identifying 300 individuals, or Pielou's evenness between substrate types (Table A.1, Table A.2.B). Therefore meio- and macrofauna communities collected from sponge settlement substrates reflected meio- and macrofauna communities assembling naturally at vents and on basalt. The usage of plastic sponges thus is an efficient way to sample the mobile meiofauna, which is typically lost when using artificial substrates such as basalt blocks or "sandwiches" which were successfully used in the past to study semi-sessile macrofaunal communities (Mullineaux et al., 2012; Susan Mills pers. obs.).

At each of the three vent sites, three settlement substrates were deployed per year (i.e. total of 9 samples in 2006). On basalt, a total of three settlement substrates were deployed per year - one each proximate to the vent site Tica, Sketchy, and P-Vent (i.e. total of 3 samples in 2006). Prior to recovery, settlement substrates were deployed for ~1 month (from Oct/Nov 2006 until Dec 2006), for ~1 year (from Dec 2006 until Nov 2007) and for ~2 years (Nov 2007 until Dec 2009). At Sketchy in 2007 and 2009, and at P-Vent in 2009, there were no vent fluid emissions and dead tubeworms were found; therefore these vent deployments were excluded from this study.

To test for the effect of deployment length, we compared settlement substrates that were deployed for 1 week, 1 month, and 3 months. We found no statistically significant effect of deployment length on abundance and diversity measures S , $S_{(m300)}$, H' log e and J' , but macrofaunal abundance and evenness were slightly greater after 1 month than after 1 week in the basalt habitat (Kruskal-Wallis; $p = 0.05$, $p = 0.05$). These results show that artificial substrates are colonized very quickly (within 1 week) and that deployment length of sponges has likely little influence on communities. Further, communities of all artificial substrate deployments (1 week, 1 month, 3 months) reflected communities assembling naturally in the axial summit trough (AST) (see Appendices Table A.1, Table A.2.A.).

All settlement substrates and natural samples were deployed and/or recovered into isolated boxes with the hydraulic arm of the submersible *Alvin*. Temperature was measured with the temperature probe of the submersible. Sulfide and pH measurements were conducted with combined potentiometric pH and sulfide sensors, as described in Mullineaux et al. (2012). Scans lasting 2 to 3 minutes (with measurements every 15 sec.) were recorded from 4 to 6 fixed locations around each

settlement substrate. The temperature, sulfide and pH ranges provide information about the degree of variation within and among our sampling sites.

For prokaryote abundances, six randomly picked 0.5 to 1.5 cm long plastic threads per sponge were removed with sterile forceps and preserved in 4% buffered formaldehyde. Each piece was dipped in autoclaved 0.2 μ m pre-filtered TE buffer for washing, put in an Eppendorf tube containing 0.5 ml of 25 % MeOH (>99.8 % (GC), Fluka), vortexed and incubated at room temperature for 15 min. Subsequently, tubes were put for up to three times in an ultrasonic bath for 1 min and vortexed again for 15 sec. An aliquot of the supernatant was diluted in TE buffer and measured with the flow cytometer. The entire procedure was repeated up to three times and extraction was stopped when cell counts in the supernatant had decreased significantly. Enumeration of prokaryotic abundance was done following Weinbauer et al. (2007).

To remove animals from substrates, each sponge (consisting of a 55 m long and 1 mm thin plastic thread woven to a loose net, which was furled and fixed with a rubber band) was uncoiled and placed into 37‰ MgCl in water for 10 minutes to relax the animals (Higgins and Thiel, 1988). Animals were then sieved through a 32 μ m and 1 mm net with 32 μ m filtered, cold seawater to separate the meio- from the (adult) macrofauna; this was repeated three times. We consider macrofauna >1 mm as adult, and macrofauna in the fraction from 32 μ m to 1 mm as juvenile. We acknowledge that not all macrofaunal specimens >1 mm were necessarily mature, but macrofaunal specimens in our samples <1 mm were very likely juveniles (Mills et al., 2007; Tyler et al., 2008). Afterwards animals were fixed in 4% buffered formaldehyde and transferred to 70% ethanol. *In situ* natural collections were treated similarly. All animals were sorted and counted (total 40,050 meio- & 60,175 macrofauna individuals) using a dissecting microscope. Abundance was standardized per sponge, which had the shape of a disk (height ~3 cm) with a circular surface area of ~64 cm². All macrofauna were identified to species level. For the meiofauna (defined as taxa that are mature at <1mm; also including protozoan foraminiferans), at least 200 individuals per higher taxon (e.g. copepods, nematodes) were identified per settlement substrate/*in situ* natural collection to species level unless fewer were found in the sample.

Species richness (S obs.), Shannon diversity ($H'_{\log e}$), and Pielou's evenness (J') were calculated from quantitative species abundance data by DIVERSE subroutines in PRIMER Version 6 package (Clarke and Gorley, 2001). Size-based rarefaction and extrapolation of species richness after identifying 300 individuals (S_{m300}) was obtained by iNEXT (Chao & Jost 2012, Hsieh et al. 2013). All calculations (S. obs. $H'_{\log e}$, J' , S_{m300}) were done for meio- and macrofauna separately, as well as

together. For statistical analyses of univariate measurements from prokaryotes and fauna at different sites and years non-parametric Kruskal-Wallis tests were conducted, and in case of significant differences post-hoc multiple comparisons (z-value) were evaluated, using the program STATISTICA (Appendice Table A.2). The SIMPROF (similarity profile) test was performed to look for statistically significant differences of clusters of sites without making any a priori hypothesis. This shows in addition to the multi-dimensional-scaling (MDS), the determination of groupings, especially when stress of the MDS is high (Clark and Warwick, 2001). One-way and two-way crossed analysis of similarity (ANOSIM) and SIMPER (similarity percentage) were used in order to determine (dis)similarity between samples from distinct years (2006, 2007, 2009, pre-eruption) and distinct habitats (tubeworm, basalt). Two-way analysis was used when testing multiple tubeworm sites per year. SIMPROF ($p < 0.05$), SIMPER, ANOSIM, and multi-dimensional-scaling (MDS) plots were performed for settlement substrates (pooled data species abundance from sponges per settlement substrate) with PRIMERv6. To create Bray-Curtis similarity matrices for these analyses, abundances of species were standardized to compensate or varying abundances, and square-root transformed to down-weight the importance of very abundant species without losing the influence of rarer species (Clarke and Gorley, 2001). We excluded foundation species (*Tevnia jerichonana*, *Riftia pachyptila*, *Bathymodiolus thermophilus*), as well as planktonic species (e.g. Calanoida, Appendicularia) in our calculations, in order make this study comparable to pre-eruption data. Dominant foundation species per site and year are provided in Table 1.

To compare recently assembled communities from tubeworm vent habitats and basalt habitats with mature communities that existed before the eruption, we compared new data with data we collected from tubeworms and basalt in 2001/02 and 2003/2004 respectively (Table 1, for details of sample collections see Gollner et al., 2015, 2010b, 2007; Govenar et al., 2005). We also use species occurrence pre-eruption data from the literature (see Gollner et al. 2010 Supplements, Gollner et al. 2015), to evaluate how many and which species had not recolonized the area after 4 years and which species were able to quickly recolonize the area. Benthic nematode data from post-eruption, which comprise $<1\%$ of specimens in this study, were previously published by Gollner et al. (2013).

2.2. Pelagic collections

For the study of species dispersal, we obtained pelagic pump samples at 3 and 75 meters above the bottom (MAB) near the vent site Sketchy in 2006 (1 x in Nov 2006, 1 x in Dec 2006), at the vent site Tica in 2006 (1 x in Nov 2006, 1 x in Dec 2006) and

2007 (3 x in Nov 2007), and at 100 meters east of Tica in 2007 (3 x in Nov 2007). The pumps were operated for 24 hours and pumped each ~40 000 liters. Trapped animals were fixed in 95% ethanol. In the lab, meiofauna was counted and identified to higher taxa. At least 200 individuals per higher meiofaunal taxon were identified to the lowest possible taxonomic level unless fewer were found in the sample. Meiofaunal species occurrences in benthic and pelagic samples are compared. Macrofaunal larvae were studied by Mullineaux, et al. (2010).

3.Results

3.1.Benthic community

Prokaryote abundances were high one year after the eruption, with mean $3.5E+11$ 64 cm^{-2} at Tica vent, $2.3E+11$ 64 cm^{-2} at P-Vent, $6.2E+10$ 64 cm^{-2} at Sketchy vent, and $2.3E+10$ 64 cm^{-2} on basalt (Table 1). Prokaryote abundance was significantly lower on basalt than at the vent sites Tica ($p = 0.003$) and P-Vent ($p < 0.001$), but similar to the vent site Sketchy ($p = 0.07$). At vents and on basalt, mean meio- and macrofauna abundances were not statistically discriminable to pre-eruption values within one year after the disturbance (vent meiofauna: 8 - 1838 ind. 64 cm^{-2} in 2006; 3 - 6246 ind. 64 cm^{-2} in 2001/02; vent macrofauna: 95 – 1600 ind. 64 cm^{-2} in 2006; 205 - 4577 ind. 64 cm^{-2} in 2001/02; basalt meiofauna 10 - 1922 ind. 64 cm^{-2} in 2006; 8 - 328 ind. 64 cm^{-2} in 2003/04; basalt macrofauna: 14 - 3351 ind. 64 cm^{-2} in 2006; 2 - 63 ind. 64 cm^{-2} in 2003/04). Overall, abundances were highly variable and were not significantly different, regardless of age, site or vent activity (Figure 3, Table 1, Table A.2).

Initial settlement was relatively quick at vents, but four years after the eruption, only about 40 % of original meio- and macrofaunal species had returned. In addition several new species could settle that were not present in the 2001/02 collections pre-eruption. Post-eruption, total meio- and macrofaunal richness was 33 each (pre-eruption 52 and 51 spp.) (see Table A.3). Most successful colonizers were species that had a broad habitat distribution and were abundant pre-eruption (Table 2). At Tica site total meiofaunal richness was similar in 2009 (26 spp.) to pre-eruption collections in 2001/02 (24 spp.), but total macrofaunal richness was lower in 2009 (19 spp.) than in 2001/02 (29 spp.) (Table 1). Meiofaunal richness in artificial settlement substrates significantly increased with time (mean S per settlement substrate in 2006: 6; 2007: 8; 2009: 17) and reached pre-eruption values by 2009 (mean S: 15) (Figure 4). Copepods contributed most to diversity. Macrofaunal richness also increased (mean S per settlement substrate in 2006: 7; 2007: 12; 2009: 12) but did not reach pre-eruption values (mean S: 25) after four years (Table 1,

Table A.2, Figure 4). A similar pattern for mean species richness was observed when we only considered the Tica site, which we followed in 2001/02, 2006, 2007, and 2009 (Table 1, Table A.2).

In the basalt habitat, community recovery of meiofauna was relatively slow. Whilst 67 % of original macrofaunal species had returned, only 28 % of original meiofaunal species were found back (see Table A.3). Post-eruption, total meio- and macrofauna richness on basalt was 30 and 29 respectively (pre-eruption 64 and 27 spp.). The low abundance but high diversity meiofauna basalt specialists were most affected by the eruption (Table 2). Meiofaunal species richness in settlement substrates did not significantly increase (mean S per settlement substrate: 9-11) from 2006 to 2009, and did not reach the pre-eruption values (mean S: 27) after four years. Macrofauna richness was similarly low on basalt pre- and post-eruption (mean S: 9-11) (Table 1, Figure 4, Table A.2.C). Interestingly, meio- and macrofaunal richnesses were similar in association with both tubeworms and on basalt after the eruption, while macrofaunal richness was significantly higher among tubeworms and meiofaunal richness was significantly higher on proximate basalt before the eruption (Table 1, Table A.2.D). Similar patterns were observed for $S_{(m300)}$ and Shannon diversity index, but were less pronounced. Pielou's evenness was similar among samples regardless of site, year, or vent activity (Table 1, Table A.2).

Within one year after the eruption, several species that were not found in pre-eruption communities had colonized the newly opened habitat. New species that reached high abundances were the limpets *Lepetodrilus tevnianus*, *Ctenopelta porifera*, and the copepod *Tisbe* sp. nov. 1 (Table 3). However, species that were abundant before the eruption at vents and on basalt (AST generalists) were most successful in recolonizing (Table 2). In 2006, most abundant species included generalists, such as the amphipod *Ventiella sulfuris*, the limpet *L. elevatus*, the polychaete *Ophryotrocha akessoni*, and the copepod *Amphiascus* sp. 1 (aff. *varians*). In addition, a few species with restricted vent distribution pre-eruption became relatively abundant in 2006, but declined in abundance in 2007 (*Aphotopontius acanthinus*, *Benthoxynus tumidiseta*, *Paralvinella pandorae*). Only by 2009, a few meiofauna basalt specialists (*Mesochra* sp. nov. 1 *Neochromadora* aff. *poecilosoma*) were able to recolonize the area (Table 3).

The MDS plot shows that community composition of meiofauna changed from 2006 to 2009, and remained dissimilar to pre-eruption communities (SIMPROF test $p < 0.05$ see Figure 5a). Among tubeworms at Tica, SIMPER dissimilarity was 82% in 2006 & 2007 (ANOSIM $R = 0.7$; $p = 0.1$), 65% in 2007 & 2009 ($R = 0.9$; $p = 0.1$). Among all tubeworm samples, SIMPER dissimilarity was 82% in 2006 & 2007 ($R =$

0.8; $p = 0.01$), and 66% in 2007 & 2009 ($R = 0.92$; $p = 0.01$). Abundance of the dirivultid copepod *Aphotopontius acanthinus* and the harpacticoid copepod *Amphiascus* sp.1 (aff. *varians*) declined with years, whilst abundance of the harpacticoid copepod *Mesochra* sp. nov. 1 and ostracods (*Thomontocypris gollnerae*, *Xylocythere vanharteni*) increased (see Table 3 for mean abundances and Table 4 for species % contributing to dissimilarity). Tubeworm communities from 2006 to 2009 remained dissimilar to pre-eruption (89 – 98 %; $R = 1$, $p = 0.01$), mainly because the pre-eruption dominant nematode *Thalassomonhystera fisheri* had hardly recovered. On basalt, similar patterns of species shifts were observed. The harpacticoid copepod *Tisbe* sp. nov. 1 and the dirivultid copepod *Benthoxynus tumidiseta* declined in abundance, whilst the harpacticoid copepod *Mesochra* sp. nov. 1 and the ostracod *Xylocythere vanharteni* increased in abundance from 2006 to 2009. Also basalt communities from 2006 to 2009 remained dissimilar to pre-eruption (e.g. 2006: 87 %; $R = 0.9$, $p = 0.03$): the foraminiferan *Abyssotherma pacifica* was more prominent pre-eruption, whilst the copepod *Tisbe* sp. nov. 1 only occurred post-eruption (see Table 3, 4). Despite these differences in the relative abundance of meiofaunal species over time, there were no significant differences among the composition of meiofaunal communities between tubeworms and basalt habitats in 2006 to 2009 in stark contrast to what was observed for mature communities pre-eruption (see SIMPROF Fig. 5; Table 4; tubeworm & basalt 2006: ANOSIM $R = -0.06$; n.s.; 2007: $R = 0.11$; n.s.; 2009: $R = 0$; n.s.; pre-eruption: $R = 0.85$; $p = 0.01$).

In contrast to meiofauna, macrofauna samples did not cluster according to years after eruption (Figure 5b). Among tubeworms, dissimilarity ranged from 34 to 54 % from 2006 to 2009 (ANOSIM $R = 0.56$ to 0.59) (Table 4). Macrofaunal species contributing most to (dis)similarity included the abundant *Ventrella sulfuris*, *Lepetodrilus tevnianus*, *L. elevatus*, and *Ophryotrocha akessoni*. The limpet *L. tevnianus* was abundant one year after eruption, and *L. elevatus* became more important two and four years after eruption (see Table 3). However, the shift in dominance of a few species (i.e. *Lepetodrilus* species change, *Ctenopelta porifera* and *Paralvinella* spp. decline) did not lead to significantly different community assemblages (Table 3, 4, SIMPROF in Fig. 5b;). Among tubeworm sites, only the site P-Vent formed a distinct cluster in 2006, since the polychaetes *Paralvinella* spp. were very dominant at this highly active vent site (for temperature and sulfide values see Table 1). The macrofaunal communities showed distinct species composition and dominance pre- and post eruption at Tica vent (2001/02 & 2009 ANOSIM $R = 1$; $p = 0.1$) and at vents in general (2001/02 & 06/09 ANOSIM $R = 0.93$; $p = 0.01$) (Table 3, 4, see SIMPROF in Fig. 5). On basalt, similar species as among tubeworms (e.g.

Lepetodrilus tevnianus and *L. elevatus*) showed some dominance shifts from 2006 to 2009 but communities remained rather similar (56 – 64 %; ANOSIM $R = 0.07 - 0.37$, $p = \text{n.s.}$) (Table 3, 4). The macrofaunal community on basalt clustered randomly among vent samples pre- and post-eruption.

3.2. Dispersal of benthic meiofauna community

Vent meiofauna were highly abundant in the water column (Figure 6). More than 17 000 individuals were sampled by pumping ~700 000 liters of seawater, including 16 380 copepods, 1340 nauplii, 104 ostracods, 60 foraminiferans and 7 nematodes. At vent sites, abundance was significantly higher at 3 MAB (meters above bottom) ($52 \pm 32 \text{ ind. } 1000^{-1}$) than at 75 MAB ($5 \pm 3 \text{ ind. } 1000^{-1}$) ($p < 0.01$). However, 100 m away from the vent site Tica, meiofaunal abundance in the water column was low ($8 \pm 8 \text{ ind. } 1000^{-1}$ in 3 m MAB; $4 \pm 3 \text{ ind. } 1000^{-1}$ in 75 MAB).

More than 95% of meiofaunal specimens in the water column were copepods. At 3 MAB, benthic copepods dominated (vent: $82 \pm 6 \%$; off-vent: $55 \pm 14 \%$), but they were less abundant 75 MAB (vent: $33 \pm 27 \%$; off-vent: $38 \pm 22 \%$). The large majority of benthic copepods were members of Dirivultidae (total 8 657 ind.) with 94% copepodites (mostly stage I), and the other 6% adults (*Aphotopontius acanthinus*, *Stygiopontius hispidulus*, *Exrma singularis*). Mean abundance of Dirivultidae in the water column was $30 \pm 18 \text{ ind. } 1000^{-1}$ at 3 MAB at vents and $< 1 \pm 1$ at 75 MAB at vents, and at 3 and 75 MAB off-vent. In contrast to the high abundance of Dirivultidae, only a few harpacticoid copepods (total 73 ind.) that were known from pre-eruption as AST generalists occurred in the water column (*Ameira* sp. 1, *Halectinosoma* sp. 1, *Xylora bathyalis*). *Tisbe* sp. 1, *Cheramyzon abyssale* and *Barathricola rimensis* were new colonizers on the benthos and were also found in the water column.

Besides the copepods, 104 ostracods (*Thomontocypris gollnerae* and unidentified juveniles) and 2 juvenile and 5 adult nematodes (*Thalassomonhystera fisheri*, *Neochromadora* aff. *poecilosoma*; *Thalassomonhystera* sp. 12 (known only from vent distant basalt)) were detected. The collected foraminiferans were non-vent species.

At the Tica site we collected pelagic samples in 2006 and 2007. In 2006, the copepods *Tisbe* sp.1 and *Aphotopontius acanthinus* were abundant (33 and 38 identified individuals) but declined in abundance by 2007 (0 and 2 identified individuals). This pattern in the water column is reflected in the benthic occurrence of these species at Tica (see also Table 3). The copepods *Ameira* sp.1, *Mesochra* sp.1, *Halectinosoma* sp.1 and *Xylora bathyalis*, as well as the nematodes

Thalassomonhystera fisheri and *Neochromadora* aff. *poecilosoma* were absent in the water column in 2006 but were present in 2007.

4. Discussion

4.1. Recovery of abundance

The rather rapid recovery of meio- and macrofauna abundance suggests that the environment is suitable to support a relatively abundant vent and basalt community soon after a major disturbance. About one year after eruption, vent sites had large aggregations of *Tevnia jerichonana* supporting an abundant associated community. The main characteristics of vent habitats, i.e. temperature, pH and sulfide ranges and their relationships, were not substantially different at our sites to levels measured among tubeworms in the same region prior the eruption (see Table 1 (Le Bris et al., 2006)). This suggests that typical ranges of abiotic constraints imposed by toxicity and corrosive properties of the diffuse flow plume remained similar and did not hinder colonization. In contrast, the sulfide-rich vent fluid likely enabled quick colonization of fauna by fueling an abundant free-living prokaryote community, the basis of the food-web of non-symbiotic vent animals (Van Dover, 2000). The high abundance of prokaryotes in the biofilm on our settlement substrates supported an abundant, diverse community during the earliest stages of community succession.

On basalt with no detectable *in situ* primary production, faunal abundances also had quickly recovered to pre-eruption values, and occasionally high abundance peaks were recorded. Prokaryote abundance was significantly lower on basalt than at the vent sites Tica and P-Vent, but similar to the vent site Sketchy, which is surprising considering the fundamental differences in energy supply between these two habitats. At Sketchy, however the low temperature and near-seawater pH measured around sponges suggest a low concentration of hydrothermal fluids. In addition, suspended particles from active vents may be transported to the vent-surrounding areas (Erickson et al., 2009), and could enhance prokaryotic growth in vent proximate areas, stimulating colonization of fauna.

4.2.1. Recovery of macrofaunal community on basalt

The macrofaunal community on basalt consisted of a primarily juvenile, low diversity but abundant subset of typical vent-associated species, suggesting that the basalt may be a nursery ground for some vent species. The proximate basalt is free of detectable hydrothermal fluid emissions, but likely obtains some input of primary production from nearby vents (Erickson et al., 2009; Govenar and Fisher, 2007). The dominance of juveniles suggests that macrofauna might obtain enough food while small but are in need of migration to more productive, nutrient-rich vent habitats to

develop into adults and reproduce (Gollner et al. in 2015). Alternatively, vent-associated macrofauna may settle on basalt and grow to a certain size until they starve to death. However, we did not encounter many empty limpet shells or other remains of dead animals.

4.2.2.Recovery of macrofaunal community at vents

At vents, macrofauna species richness significantly increased during the four years after the volcanic eruption, suggesting that several species can recover well from local major disturbance events. However, only half of macrofaunal species had returned to the study area within four years, indicating incomplete recovery and possible loss of species. Following eruptions at Juan de Fuca Ridge, 24 out of 25 and 27 out of 36 taxa had returned after 2, and 3 years respectively (Marcus et al., 2009; Tunnicliffe et al., 1997). After the 1991 eruption at 9°50'N EPR, the number of mega- and macrofaunal taxa reached 31 out of ~43 from a regional species pool five years after eruption (Shank et al., 1998; Van Dover, 2011). After the 2006 eruption at 9°50'N EPR, 33 from the regional species pool of 51 macrofaunal species (excluding foundation species *Alvinella caudata*, *A. pompejana*, *Bathymodiolus thermophilus* with *Branchipolynoe symmytilida*, *Tevnia jerichonana*, *Oasisia alvinae*, and *Riftia pachyptila*) had returned by 2010. The higher regional species pool number pre 2006 eruption (Gollner et al. 2015) compared to the ~43 species pre 1991 eruption (Shank et al. 1998) may be explained by the greater sampling effort of *in situ* collections by Gollner et al. (2015) versus the photographic survey by Shank et al. (1998) and the associated finding of more rare species. This indicates that especially rare macrofaunal species may be most threatened by major disturbance events.

Rare species of mature communities might have fundamental roles in early successional stages at deep-sea hydrothermal vents. The limpet *Lepetodrilus tevnianus* was extremely rare in mature pre-eruption communities but was abundant in our samples during early succession in 2006 and 2007. Mullineaux et al. (2010, 2012) observed the same pattern and suggested that this pioneer species possibly outcompetes the ubiquitous pre-eruption congener *L. elevatus* in immediate post-eruption habitat. They also questioned whether this could be an alternative stable state. However, in 2009, abundance of *L. tevnianus* declined and *L. elevatus* became more abundant, suggesting a successional sequence of these species as the environment changed. The mature tubeworm community samples from pre-eruption formed a distinct cluster in our MDS-plot, likely due to the presence of more rare species.

4.2.3.Recovery of meiofaunal community at vents

The meiofauna exhibited a shift in community composition within the first four years, reflecting the distinct dispersal mechanisms of meiofauna taxa. Vent-adapted species, namely dirivultid copepods dominated in the water column with their copepodite stages and as adults in the benthos in 2006, indicating high dispersal abilities. Dirivultidae are highly specialized to vents, i.e. have evolved distinct feeding-niches at vents, have developed high hemoglobin concentrations with a high and temperature sensitive oxygen affinity to live in low oxygen environments, and have a restricted distribution to vents and the AST along mid ocean ridges (Gollner et al., 2010a; Hourdez et al., 2000; Limén et al., 2008). Thus, being specialized and restricted to vents in a similar way to the macrofauna, they need to be able to migrate/disperse between patchy distributed vent sites as the macrofauna do. Mean abundances of 30 dirivultids per 1000 l at 3 meters above vent bottom (MAB) were even higher than values reported for gastropod and polychaete larvae in the same area at 4 MAB (ranges from ~2 – 11 ind. per 1000 l) (Beaulieu et al., 2009). Thus, the finding of thousands of dirivultid copepodites in the water column and genetic data on dirivultids (Gollner et al., 2011) support the assumption of high dispersal capacity which likely enabled them to quickly colonize the 9°50'N EPR area after the volcanic eruption.

Further, some pioneers could profit from the eruption. The copepods *Tisbe* sp.1, *Cheramyzon abyssale* and *Barathricola rimensis* were unknown from the area pre-eruption but were abundant in the water column and in the vent and basalt benthic zone in 2006. However by 2007, abundances of these three species declined, whilst other harpacticoid copepods, had replaced them. This pattern was observed at vent and basalt areas, suggesting that the shift was not directly caused by abiotic changes such as hydrothermal fluid flow composition, but could still relate to changes in productivity over the years. Alternatively, these copepods might be pioneer species that have distinct life history traits such as good dispersal potential but are competition poor.

In 2007, copepod species with a broad distribution range but more limited dispersal could become more abundant. For example, the copepod *Amphiascus* sp. 1 (aff. *varians*) was prominent. Other harpacticoid copepods that are considered AST generalists (e.g. *Ameira* sp. 1) were detected in low abundance in the water column and were also present in the benthic zone. We hypothesize that AST generalists can both migrate along basalt and disperse as adults or as juveniles via the water column to recolonize newly formed basalt and vent areas following an eruption.

In 2009, community composition remained different to pre-eruption. Harpacticoid copepods with rather limited distribution pre-eruption (e.g. *Mesochra* sp.

nov. 1) could now colonize in greater numbers. Nematodes, which lack a dispersal stage, were like in 2006 and 2007 still extremely low in abundance and richness. Gollner et al. (2013) stated that nematodes were extremely influenced by this volcanic eruption and hypothesized that harsh physico-chemical conditions such as at P-Vent, and the large extent of the disturbance and thus distant source populations hindered a successful nematode colonization. Also Copley et al. (2007) hypothesized that the higher nematode dominance in older mussel beds at EPR vents was consistent with lower dispersal capability and therefore longer colonization time for vent nematodes. With our new finding of just 7 nematodes out of >17 000 meiofaunal specimens in the pelagic collections, we show that vent nematodes may be poor dispersers and are thus extremely threatened by major disturbance events.

Pre-eruption, one nematode species and a diverse community of the vent-endemic dirivultid copepods dominated among tubeworms, and harpacticoid copepods and ostracods were rare (Gollner et al., 2007). In 2009, at the same study site (Tica), similar species occurred but harpacticoid copepods and ostracods were more prominent. The dominant pre-eruption nematode *Thalassomonhystera fisheri* (>60% of the meiofaunal community at Tica in 2001/2002) was not found there in 2009, although it occurred in low abundance at other sites. This shift in dominance could have been caused by slightly different abiotic habitat characteristics. In 2009, the temperature maximum around sponges (max. 19°C) was lower than the temperature determined at Tica in 2001 (max. 32°C) (Le Bris et al., 2006). In a meiofaunal study on various hydrothermal vent regimes in the 9°50'N region of the EPR area, dirivultid copepods dominated at more extreme vent regimes, while harpacticoids were more prominent at lower temperature vent regimes (Gollner et al., 2010b). The lack of dominance of nematodes may be further influenced by the poor dispersal capabilities of nematodes, which do not have a special dispersal stage (Higgins and Thiel, 1988).

4.2.4.Recovery of meiofaunal community on basalt

No species increase was found on basalt during the studied post-eruption time pointing to low recolonization potential of basalt specialists. The pre-eruption meiofaunal basalt community was characterized by the presence of several AST generalists and many rare basalt specialists (Gollner et al., 2010b). After the eruption, AST generalists such as the copepod *Amphiascus* sp. 1 could quickly colonize both vents and basalt. However, the very first basalt specialists were not recorded until 2009, and the large majority of specialists had not returned. Two factors could explain this pattern. First, basalt specialists occur in low abundances and thus produce proportionally fewer offspring that could invade the disturbed area.

Second, many of the basalt-specialists were nematodes, which are considered poor dispersers, prolonging a reestablishment of the nematode communities after eruption.

5. Conclusions and implications for conservation

The dispersal ability of organisms is a key trait to determine metacommunity structure (De Bie et al., 2012) and influences the recovery of vent and basalt habitats after an eruption. While species richness recovery was rather quick but incomplete at hydrothermal vents, slower recovery was observed on basalt. Vent fields are patchily distributed and isolated from each other and recolonization via dispersal of planktonic larvae is vital for the persistence of populations. Hence, the arrival of macrofaunal species from distant non-disturbed vent areas had a strong influence on the succession (Mullineaux et al., 2010, 2012). The dirivultid copepods with special adaptations to the vent environment and high dispersal capacities were successful in quickly recolonizing vent fields. In contrast to vents, basalt areas are semi-continuous hard-substrate environments. Only a few adult macrofauna specimens were found on basalt, but the vent macrofauna might use this surrounding area as a nursery for juveniles. The meiofauna on basalt is a diverse community of predominantly basalt specialists, but also generalists that can live in both basalt and vent habitats. The basalt specialists were most affected by the disturbance, based on our observation that the majority of species had not recolonized the area after four years. These specialists were low in abundance and were not found in the plankton, suggesting limited dispersal and colonization capacities. Almost nothing is yet known about the biogeography or life cycles of basalt species, prohibiting the establishment of a realistic management plan.

The successional pattern differed among the meio- and the macrofauna at vents and on basalt. The vent megafauna switched within the 4 studied years from a *Tevnia* to a *Riftia* dominated community. The associated macrofauna showed some change in community composition: *Lepetodrilus tevnianus* shifted to *L. elevatus*, *Ctenopelta porifera* and *Paralvinella* spp. declined in abundance. In contrast, the meiofaunal community showed a stronger successional sequence, where first colonizers were dirivultid copepods, followed by generalistic harpacticoid copepods, ostracods, and nematodes. The meiofauna succession at vents is likely influenced by the distinct dispersal abilities of meiofauna taxa, with excellent dirivultid dispersers and poor nematode dispersers. On basalt, macrofauna showed no obvious succession, likely because the species were juveniles of typical vent species, which have high dispersal abilities and relatively quickly recolonized the area. In contrast, the meiofauna on basalt showed a successional sequence of species according to

their presumed dispersal potential (dirivultids, harpacticoids, nematodes). However, most of the rare basalt specialists had not returned after the 4 year study period.

The different faunal recovery patterns of vent and proximate basalt habitats, which are in accordance with their distinct faunal life-history traits suggest distinct management strategies to mitigate future mining effects. We suggest that determination of natural conservation units for key species should include vent restricted species (e.g. foundation species with symbionts such as *Riftia pachyptila*) as well as non-symbiotic associated vent fauna (e.g. limpets) that may use the non-vent areas as a nursery. To capture the recovery of proximate basalt areas, species with a broad habitat range (e.g. harpacticoid copepods) as well basalt specialists (e.g. nematodes) should be regarded. We further suggest that the identification of conservation areas should include distant vent fields for the vent ecosystems. In contrast, limitation of on-site mined area size should allow mitigation of mining effects on neighboring deep-sea communities.

Last, we like to stress that there is a dearth of baseline knowledge on fauna from vent-associated areas as well as inactive vent areas, although both will likely be affected by future mining operations. In addition, all studies on community assembly after seafloor eruptions have been conducted on intermediate to fast-spreading plate boundaries (Marcus et al., 2009; Mullineaux et al., 2012; Shank et al., 1998; Tunnicliffe et al., 1997) where vent fields are separated by a few kilometers and persist on time scales of years to decades (Haymon et al., 1991; Lutz et al., 2008; Shank et al., 1998). Virtually nothing is known on the recovery of faunal communities on slow spreading centers, where vent fields are separated by several 100 km (German et al., 1996; Murton et al., 1994). Larval dispersal is affected by geological settings and populations show high connectivity at slow spreading centers (Beedessee et al., 2013). However, dynamic community change is slow at slow spreading centers and no successional sequences were observed on decadal scale on sites at the Mid Atlantic Ridge (Cuvelier et al. 2011, Gebruk et al. 2010). Thus, resilience might be lower and recovery might be slower at slow spreading centers, since communities are adapted to persist for several decades or even centuries. In order to mitigate mining impacts in the future, more research is needed on dispersal and recovery mechanisms of communities from slow spreading ridges, as well as from neighboring deep-sea habitats and inactive sulfide deposits.

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889 **TABLES**

890

891

892 Table 1. Habitat characteristics of tubeworm sites Tica, Sketchy, and P-Vent, and of bare basalt one (1), two (2), and four (4) years after
893 eruption. In addition, published pre-eruption data from tubeworm sites Tica and Riftia Field are shown (Gollner et al. 2010; 2015). Age of
894 communities at time of sampling is given (i.e. Tica1 communities were 1 year old in 2006 after the eruption in 2005/06; Basalt pre-eruption
895 communities were 12 years old in 2003 after the eruption in 1991). Maximal temperatures were recorded at recovery of settlement substrates,
896 brackets (*) show values measured at deployment. Three settlement substrates were deployed at each site. Mean prokaryote abundance, total
897 faunal abundance (ab.) per 64 cm⁻², relative abundance of juvenile meio- and macrofauna, species richness (S obs.), size-based rarefaction
898 and extrapolation of species richness after identifying 300 individuals (S_(m300)), Shannon-diversity (H'loge), Pielou's evenness (J'), and total
899 richness are given for entire faunal communities (meio- and macrofauna (MEMA)), meiofauna (ME), and macrofauna (MA).
900

	Tica1	Tica2	Tica4	Sketchy1	P-Vent1	P-Vent2	Basalt1	Basalt2	Basalt4	Tica pre- eruption	Tica & Rifta Field pre-eruption	Basalt pre- eruption
age (years)	1	2	4	1	1	2	1	2	4	>6	>6	12 to 13
year of sampling	2006	2007	2009	2006	2006	2007	2006	2007	2009	2001-2002	2001-2002	2003-2004
number of samples	3	3	3	3	3	3	3	3	3	3	6	4
max. T (°C)	16 (27*)	15	19 ^y	3 (12*)	28 (27*)	18	3	2	2	32	32-54	2
mean T (°C)	5 to 9			3 to 4	14-29	14-Feb	2 to 3					2
mean H2S	0 -23 ^x			n.i.	96-473	0-115	0-3			max. 283	max. 85-283	0
mean pH	6.9-7.4			7.3-7.9	5.9-7.4	6.1-7.6	7.4-8			min 5.7	min 4.4-5.7	~8
foundation species	<i>Tevnia</i>	<i>Tev & Rif</i>	<i>Riftia</i>	<i>Tevnia</i>	bacteria	<i>Tevnia</i>	no	no	no	<i>Riftia</i>	<i>Riftia</i>	no
prokaryote ab.	3.50E+11			6.20E+10	2.30E+11		2.30E+10					
MEMA ab.	443 ± 204	789 ± 736	554 ± 212	922 ± 695	1067 ± 840	1333 ± 162	184 ± 38	2193 ± 1884	2189 ± 3263	5390 ± 3080	2922 ± 3326	134 ± 174
ME Ab.	43 ± 17	37 ± 20	213 ± 224	14 ± 11	937 ± 804	9 ± 5	77 ± 64	670 ± 1084	1623 ± 2599	2255 ± 3459	1142 ± 2504	113 ± 147
ME % juveniles ab.	27 ± 35	68 ± 11	19 ± 7	32 ± 9	1 ± 1	1 ± 2	22 ± 17	51 ± 16	41 ± 28	2 ± 3	6 ± 6	5 ± 3
MA ab.	399 ± 220	752 ± 752	342 ± 209	908 ± 695	131 ± 37	1324 ± 162	107 ± 102	1523 ± 1691	566 ± 685	3125 ± 1261	1780 ± 1681	21 ± 28
MA % juveniles ab.	18 ± 10	27 ± 8	55 ± 12	36 ± 5	22 ± 5	30 ± 9	63 ± 2	82 ± 17	75 ± 20	2 ± 3	9 ± 9	69 ± 37
MEMA S (obs.)	13 ± 4	22 ± 3	29 ± 6	15 ± 2	11 ± 5	17 ± 0	18 ± 6	23 ± 8	23 ± 9	39 ± 7	39 ± 7	36 ± 12
ME S (obs.)	5 ± 4	10 ± 4	17 ± 5	7 ± 1	6 ± 3	5 ± 1	9 ± 3	12 ± 4	13 ± 4	16 ± 5	15 ± 6	27 ± 6
MA S (obs.)	8 ± 1	12 ± 1	12 ± 2	7 ± 2	5 ± 2	12 ± 1	9 ± 4	11 ± 4	10 ± 7	23 ± 4	25 ± 3	9 ± 5
MEMA S(m300)	10 ± 4	15 ± 7	22 ± 7	9 ± 2	10 ± 4	9 ± 2	16 ± 6	15 ± 7	21 ± 4	15 ± 5	18 ± 5	36 ± 7
ME S(m300)	6 ± 5	14 ± 7	20 ± 3	11 ± 3	7 ± 3	6 ± 1	11 ± 3	12 ± 1	12 ± 4	15 ± 4	14 ± 4	30 ± 5
MA S(m300)	6 ± 1	9 ± 3	11 ± 3	6 ± 1	5 ± 2	7 ± 1	13 ± 8	8 ± 4	10 ± 6	12 ± 4	14 ± 3	12 ± 6
MEMA H'(loge)	1.1 ± 0.5	1.2 ± 0.7	2.0 ± 0.8	1.2 ± 0.2	1.1 ± 0.4	0.9 ± 0.4	1.6 ± 0.5	1.3 ± 0.6	2.0 ± 0.4	1.6 ± 0.4	1.9 ± 0.5	2.2 ± 0.6

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ME H'(loge)	0.5 ± 0.5	1.6 ± 0.1	1.9 ± 0.3	1.7 ± 0.1	0.7 ± 0.5	1.4 ± 0.11	1.4 ± 0.4	1.3 ± 0.5	1.8 ± 0.4	1.0 ± 0.5	1.4 ± 0.6	1.9 ± 0.7
MA H'(loge)	0.7 ± 0.3	0.9 ± 0.5	1.2 ± 0.5	1.1 ± 0.1	0.8 ± 0.4	0.9 ± 0.4	1.5 ± 0.2	0.7 ± 0.2	1.2 ± 0.1	1.4 ± 0.2	1.8 ± 0.4	1.3 ± 0.2
MEMA J'	0.4 ± 0.2	0.4 ± 0.2	0.6 ± 0.2	0.4 ± 0.1	0.5 ± 0.1	0.3 ± 0.2	0.6 ± 0.1	0.4 ± 0.3	0.7 ± 0.1	0.4 ± 0.1	0.5 ± 0.1	0.6 ± 0.2
ME J'	0.3 ± 0.2	0.7 ± 0.2	0.7 ± 0.1	0.9 ± 0.1	0.4 ± 0.2	0.9 ± 0.1	0.7 ± 0.2	0.5 ± 0.2	0.7 ± 0.1	0.4 ± 0.2	0.6 ± 0.3	0.6 ± 0.3
MA J'	0.4 ± 0.2	0.4 ± 0.2	0.5 ± 0.2	0.5 ± 0.1	0.5 ± 0.2	0.3 ± 0.2	0.7 ± 0.1	0.3 ± 0.2	0.6 ± 0.2	0.5 ± 0.1	0.5 ± 0.1	0.7 ± 0.3
ME total S	9	17	26	10	10	8	17	21	18	24	31	64
MA total S	11	15	19	11	7	15	14	20	20	29	35	31

905 Table 2: Mean relative abundance ($\pm$ stdv) and total number of meio- and macrofauna species pre-eruption (2001-2004) and post-eruption
906 (2006, 2007, 2009) classified after habitat occurrence. AST (Axial Summit Trough): species occurred at vents and on basalt; BS (basalt
907 specialist): species occurred only on basalt; VG (vent generalist): species occurred in at least two vent habitats; VS (vent specialist): species
908 occurred only in a single vent habitat; NEW: species not present in 2001-04 collections. In addition, numbers of species (of settlement
909 substrates and control samples) that had not returned to the area by 2009 are given.
910

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	2001-04	2006	2007	2009	2001-04	2006	2007	2009	not returned
	rel. ab %	rel. ab %	rel. ab %	rel. ab %	species	species	species	species	species
meiofauna									
AST	84 $\pm$ 14	41 $\pm$ 28	78 $\pm$ 20	67 $\pm$ 7	29	13	13	14	11
VG	4 $\pm$ 6	30 $\pm$ 40	16 $\pm$ 20	6 $\pm$ 5	12	2	3	4	7
VS	4 $\pm$ 9	15 $\pm$ 2	0	0	11	1			9
BS	9 $\pm$ 2	0	0.5 $\pm$ 1	23 $\pm$ 9	35		2	4	29
NEW		15 $\pm$ 15	6 $\pm$ 7	4 $\pm$ 4		5	6	9	
macrofauna									
AST	90 $\pm$ 7	61 $\pm$ 35	95 $\pm$ 5	89 $\pm$ 17	22	9	16	12	4
VG	6 $\pm$ 8	5 $\pm$ 10	1 $\pm$ 1	1 $\pm$ 2	19	2	3	3	7
VS	1 $\pm$ 3	20 $\pm$ 24	1 $\pm$ 2	0.01 $\pm$ 0.01	10	2	2	3	6
BS	2 $\pm$ 4	0	0	0	5				6
NEW		15 $\pm$ 13	3 $\pm$ 5	10 $\pm$ 18		6	7	8	

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915 Table 3: Mean abundance ($\pm$ stdv) per 64 cm⁻² of meio- and macrofaunal species that were contributing most to SIMPER dissimilarities (see
916 Table 4) at tubeworm (t) and basalt (b) sites in different years. Taxon (C – Copepoda, N – Nematoda, O – Ostracoda, M – Mollusca, P –
917 Polychaeta, A – Amphipoda) is given for each species. Habitat type is given for each species according to Gollner et al. 2010 & 2015: AST
918 (Axial Summit Trough): species occurred at vents and on basalt; BS (basalt specialist): species occurred only on basalt; VG (vent generalist):
919 species occurred in at least two vent habitats; VS (vent specialist): species occurred only in a single vent habitat; NEW: species was recorded
920 for the first time at the studied sites)). Please note that types can change after analyzing new samples; e.g. the former basalt specialist
921 *Mesochra* sp. nov. 1 was found among tubeworms post-eruption. **Amphiascus* was found at mussels and basalt pre-eruption.
922

	taxon	type	t-2001/02	t-2006	t-2007	t-2009	b-2003/04	b-2006	b-2007	b-2009
meiofauna										
<i>Cheramyzon abyssale</i>	C	new			0.1 $\pm$ 0.2	0.2 $\pm$ 0.3		0.3 $\pm$ 0.4	1 $\pm$ 2	10 $\pm$ 16
<i>Tisbe</i> sp. nov. 1	C	new		4 $\pm$ 6	1 $\pm$ 2	1 $\pm$ 1		12 $\pm$ 15	1 $\pm$ 2	
<i>Amphiascus</i> sp. 1 (<i>aff. varians</i>)	C	AST	0*	7 $\pm$ 14	7 $\pm$ 9	4 $\pm$ 5	0.5 $\pm$ 0.4	15 $\pm$ 21	42 $\pm$ 65	5 $\pm$ 8
<i>Thalassomonhystera fisheri</i>	N	AST	1006 $\pm$ 2298	0.3 $\pm$ 0.7	0.3 $\pm$ 0.4		1 $\pm$ 1	1 $\pm$ 1	10 $\pm$ 9	1 $\pm$ 2
<i>Thomontocypris gollnerae</i>	O	AST	0.03 $\pm$ 0.07	0.3 $\pm$ 0.6	0.4 $\pm$ 0.4	51 $\pm$ 38	0.1 $\pm$ 0.1	1 $\pm$ 1	2 $\pm$ 3	245 $\pm$ 424
<i>Xylocythere vanharteni</i>	O	AST	0.2 $\pm$ 0.3	0.1 $\pm$ 0.2	2 $\pm$ 1	3 $\pm$ 3	0.1 $\pm$ 0.2	0.1 $\pm$ 0.1	521 $\pm$ 898	76 $\pm$ 125
<i>Aphotopontius acanthinus</i>	C	VG	2 $\pm$ 4	93 $\pm$ 209	0.4 $\pm$ 0.5	2 $\pm$ 3		0 2 $\pm$ 1	1 $\pm$ 1	
<i>Benthoxyne tumidiseta</i>	C	VS	4 $\pm$ 9	131 $\pm$ 337				0 26 $\pm$ 46		
<i>Neochromadora aff. poecilosoma</i>	N	BS			0.2 $\pm$ 0.4	7 $\pm$ 6	1 $\pm$ 1			31 $\pm$ 42
<i>Mesochra</i> sp. nov. 1	C	BS			0.2 $\pm$ 0.4	32 $\pm$ 40	2 $\pm$ 5		1 $\pm$ 2	238 $\pm$ 378
macrofauna										
<i>Ctenopelta porifera</i>	M	new		3 $\pm$ 1	0.2 $\pm$ 0.4	1 $\pm$ 2			4 $\pm$ 6	
<i>Lepetodrilus tevnianus</i>	M	new		71 $\pm$ 5	5 $\pm$ 5			22 $\pm$ 29	0.3 $\pm$ 0.4	4 $\pm$ 7
<i>Lepetodrilus elevatus</i>	M	AST	917 $\pm$ 1031	41 $\pm$ 59	16 $\pm$ 11	45 $\pm$ 8	2 $\pm$ 2	36 $\pm$ 39	7 $\pm$ 10	53 $\pm$ 87
<i>Ophryotrocha akessoni</i>	P	AST	27 $\pm$ 20	14 $\pm$ 13	73 $\pm$ 52	33 $\pm$ 8	1 $\pm$ 2	8 $\pm$ 2	338 $\pm$ 287	167 $\pm$ 229
<i>Ventiella sulfuris</i>	A	AST	235 $\pm$ 273	297 $\pm$ 386	817 $\pm$ 529	198 $\pm$ 230	11 $\pm$ 22	27 $\pm$ 41	533 $\pm$ 920	33 $\pm$ 51
<i>Paralvinella pandorae</i>	P	VS	14 $\pm$ 15	30 $\pm$ 45	14 $\pm$ 17	0.2 $\pm$ 0.3		0 1 $\pm$ 1		

923

924 Table 4. Dissimilarity (ANOSIM R & p, SIMPER dissimilarity (%) and first three species that contributed most to dissimilarity) among all
925 tubeworm (t) sites, Tica vent site, and basalt (b) in different years. In addition, information on dissimilarity between tubeworm and basalt habitat
926 is given.
927

meiofauna	ANOSIM		SIMPER	
tubeworms & years	R	p	dissim.	species
t-2001/02 & t-2006	1	0.01	97	<i>Thalassomonhystera fisheri</i> (24 %), <i>Aphotopontius acanthinus</i> (18 %), <i>Halomonhystera hickeyi</i> (7 %)
t-2001/02 & t-2009	1	0.1	89	<i>Thalassomonhystera fisheri</i> (18 %), <i>Thomontocypris gollnerae</i> (12 %), <i>Mesochra</i> sp. nov. 1 (8 %)
t-2006 & t-2007	0.815	0.01	82	<i>Aphotopontius acanthinus</i> (16 %), <i>Amphiascus</i> sp. 1 (aff. <i>varians</i>) (13 %), <i>Xylocythere vanharteni</i> (10 %)
t-2007 & t-2009	0.92	0.01	66	<i>Amphiascus</i> sp. 1 (aff. <i>varians</i>) (16 %), <i>Thomontocypris gollnerae</i> (13 %), <i>Mesochra</i> sp. nov. 1 (9 %)
Tica vent site & years				
Tica-2001/02 & Tica-2006	1	0.01	97	<i>Thalassomonhystera fisheri</i> (24 %), <i>Aphotopontius acanthinus</i> (18 %), <i>Halomonhystera hickeyi</i> (7 %)
Tica-2001/02 & Tica-2009	1	0.01	91	<i>Thalassomonhystera fisheri</i> (18 %), <i>Thomontocypris gollnerae</i> (12 %), <i>Mesochra</i> sp. nov. 1 (7 %)
Tica-2006 & Tica-2007	0.704	0.1	82	<i>Aphotopontius acanthinus</i> (22 %), <i>Amphiascus</i> sp. 1 (aff. <i>varians</i>) (15 %), <i>Ameira</i> sp. nov. 1 (13 %)
Tica-2007 & Tica-2009	0.93	0.1	65	<i>Amphiascus</i> sp. 1 (aff. <i>varians</i>) (17 %), <i>Thomontocypris gollnerae</i> (12 %), <i>Mesochra</i> sp. nov. 1 (9 %)
basalt & years				
b-2001/02 & b-2006	0.926	0.03	87	<i>Abyssotherma pacifica</i> (10 %), <i>Tisbe</i> sp. nov. 1 (9 %), <i>Amphiascus</i> sp. 1 (aff. <i>varians</i>) (7 %)
b-2001/02 & b-2009	0.463	0.11	74	<i>Mesochra</i> sp. nov. 1 (9 %), <i>Abyssotherma pacifica</i> (7 %), <i>Ameira</i> sp. nov. 1 (6 %)
b-2006 & b-2007	0.296	0.2	73	<i>Xylocythere vanharteni</i> (12 %), <i>Tisbe</i> sp. nov. 1 (10 %), <i>Benthoxynus tumidiseta</i> (8 %)
b-2007 & b-2009	0.519	0.1	73	<i>Mesochra</i> sp. nov. 1 (11 %), <i>Amphiascus</i> sp. 1 (aff. <i>varians</i>) (9 %), <i>Xylocythere vanharteni</i> (9 %)
tubeworms & basalt				
t-2001/02 & b 2003/04	0.85	0.01	83	<i>Thalassomonhystera fisheri</i> (9 %), <i>Abyssotherma pacifica</i> (7 %), <i>Scotoecetes introrsus</i> (6 %)
t-2006 & b-2006	-0.06	0.66	70	<i>Benthoxynus tumidiseta</i> (18 %), <i>Amphiascus</i> sp. 1 (aff. <i>varians</i>) (15 %), <i>Aphotopontius acanthinus</i> (14 %)
t-2007 & b-2007	0.11	0.26	77	<i>Xylocythere vanharteni</i> (17 %), <i>Amphiascus</i> sp. 1 (aff. <i>varians</i>) (14 %), <i>Halomonhystera hickeyi</i> (9 %)
t-2009 & b-2009	0	0.1	53	<i>Ameira</i> sp. nov. 1 (13 %), <i>Thomontocypris gollnerae</i> (12 %), <i>Mesochra</i> sp. nov. 1 (8 %)
macrofauna	ANOSIM		SIMPER	
tubeworms & years	R	p	dissim.	species
t-2001/02 & t-2006	1	0.01	67	<i>Lepetodrilus elevatus</i> (18 %), <i>Ventiella sulfuris</i> (16 %), <i>Lepetodrilus tevnianus</i> (11 %)
t-2001/02 & t-2009	0.93	0.01	53	<i>Ventiella sulfuris</i> (13 %), <i>Lepetodrilus elevatus</i> (11 %), <i>Ophryotrocha akessoni</i> (11 %)
t-2006 & t-2007	0.59	0.01	54	<i>Ventiella sulfuris</i> (22 %), <i>Paralvinella pandorae</i> (21 %), <i>Dahlella caldariensis</i> (11 %)
t-2007 & t-2009	0.59	0.01	42	<i>Lepetodrilus elevatus</i> (16 %), <i>Ventiella sulfuris</i> (10 %), <i>Dahlella caldariensis</i> (9 %)
Tica vent site & years				
Tica-2001/02 & Tica-2006	1	0.1	68	<i>Lepetodrilus elevatus</i> (18 %), <i>Ventiella sulfuris</i> (16 %), <i>Lepetodrilus tevnianus</i> (11 %)
Tica-2001/02 & Tica-2009	1	0.1	58	<i>Lepetodrilus elevatus</i> (15 %), <i>Ophryotrocha akessoni</i> (14 %), <i>Ventiella sulfuris</i> (10 %)

Tica-2006 & Tica-2007	0.56	0.2	34	<i>Lepetodrilus tevnianus</i> (17 %), <i>Dahlella caldariensis</i> (14 %), <i>Ophryotrocha akessoni</i> (12 %)
Tica-2007 & Tica-2009	0.58	0.1	47	<i>Ophryotrocha akessoni</i> (13 %), <i>Ventiella sulfuris</i> (13 %), <i>Lepetodrilus elevatus</i> (10 %)
basalt & years				
b-2001/02 & b-2006	0.2	0.17	80	<i>Lepetodrilus elevatus</i> (10 %), <i>Leptodrilus tevnianus</i> (10 %), <i>Amphisamytha galapagensis</i> (9 %)
b-2001/02 & b-2009	0.11	0.29	76	<i>Ophryotrocha akessoni</i> (16 %), <i>Lepetodrilus elevatus</i> (10 %), <i>Amphisamytha galapagensis</i> (10 %)
b-2006 & b-2007	0.37	0.2	64	<i>Lepetodrilus elevatus</i> (16 %), <i>Ophryotrocha akessoni</i> (15 %), <i>Lepetodrilus tevnianus</i> (14 %)
b-2007 & b-2009	0.07	0.4	56	<i>Leptodrilus elevatus</i> (15 %), <i>Ventiella sulfuris</i> (15 %), <i>Clypeosectus delectus</i> (11 %)
tubeworms & basalt				
t-2001/02 & b 2003/04	0.61	0.01	72	<i>Lepetodrilus elevatus</i> (12 %), <i>Amphisamytha galapagensis</i> (9 %), <i>Ventiella sulfuris</i> (8 %)
t-2006 & b-2006	-0.01	0.39	61	<i>Ventiella sulfuris</i> (23 %), <i>Lepetodrilus elevatus</i> (17 %), <i>Lepetodrilus tevnianus</i> (14 %)
t-2007 & b-2007	0.71	0.01	59	<i>Ventiella sulfuris</i> (30 %), <i>Ophryotrocha akessoni</i> (12 %), <i>Dahlella caldariensis</i> (12 %)
t-2009 & b-2009	0.37	0.1	63	<i>Ventiella sulfuris</i> (28 %), <i>Lepetodrilus elevatus</i> (17 %), <i>Ophryotrocha akessoni</i> (8 %)

929 **FIGURES**

930

931 Figure 1: Vent sites Tica, P-Vent, and Sketchy on the East Pacific Rise. Several km² (blue outline) of the area were flooded with lava during an
932 eruption in 2005/2006. Map courtesy of S.A. Soule (Soule et al. 2007).

933

934 Figure 2. (a) Vent site colonized by tubeworm foundation species *Riftia pachyptila* and *Tevnia jerichonana* at Tica in 2009. (b) Basalt proximate
935 to the vent site Tica in 2006. Settlement substrate consists of plastic kitchen sponges (circle surface area of one sponge equals $\sim 64 \text{ cm}^2$).
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940 Figure 3. Abundance (individuals per sponge; equals $\sim 64 \text{ cm}^2$; mean $\pm$ stdv) of meiofauna (left) and macrofauna (right) at tubeworm sites (a &
 941 b) and on basalt (c & d) before eruption in 2001-2004 and after eruption in 2006, 2007, and 2009. Jagged line separates pre- and post-eruption
 942 and points out the volcanic eruption in 2005/06 which killed all fauna at the here studied sites. Letters shared in common indicate no significant
 943 differences ($p > 0.05$); square: mean; box: SE; whiskers: SD.

945 Figure 4. Observed species richness S (obs.) (mean $\pm$ stdv) of meiofauna (left) and macrofauna (right) at tubeworm sites (a & b) and on bare
 946 basalt (c & d) before eruption in 2001-2004 and after eruption in 2006, 2007, and 2009. Jagged line separates pre- and post-eruption and
 947 points out the volcanic eruption in 2005/06 which killed all fauna at the here studied sites. Letters shared in common indicate no significant
 948 differences ($p > 0.05$); square: mean; box: SE; whiskers: SD.
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952 Figure 5. MDS plot based on Bray-Curtis similarity from relative species abundance data for meiofauna (left) and macrofauna (right)
 953 communities from tubeworm samples (t) and bare basalt samples (b). Data are from before eruption in 2001-2004 and after eruption in 2006,
 954 2007, and 2009. Circles indicate similar community composition of groups (SIMPROF test $p < 0.05\%$).
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964 Figure 6. Meiofaunal abundance (mean $\pm$ stdv ; ind. per 1000 liter) in pelagic collections 3 meters (Figure 5a) and 75 meters (Figure 5b) above
 965 bottom at the vent site Sketchy (collected in 2006), the vent site Tica (collected in 2006 and 2007), and in 100 meters east off the vent-site Tica
 966 (off-vent; collected in 2007). Square: mean; box: SE; whiskers: SD.
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971 **APPENDICES**

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973 Table A.1. Mean $\pm$ stdv of total faunal abundance (ab.) per 64 cm⁻², species richness (S obs.), expected number of species (S(m300)),
 974 Shannon-diversity (H'loge), and Pielou's evenness (J') are given for the entire faunal community (meio and macrofauna (MEMA)), the
 975 meiofauna (ME), and the macrofauna (MA) for all control samples. Controls were performed to test the influence of sponge deployment length
 976 (1 week, 1 month, 3 months) and to test the suitability of sponges as settlement substrates. For the latter, *in situ* samples of natural
 977 communities at vents and on basalt were collected.
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CONTROL	deployment length	deployment length	deployment length	deployment length	deployment length	<i>in situ</i>	<i>in situ</i>	<i>in situ</i>
vent/basalt	vent	vent	vent	basalt	basalt	vent	basalt	basalt
deployment length/ <i>in situ</i>	1 week	1 month	3 months	1 week	1 month	<i>in situ</i>	<i>in situ</i>	<i>in situ</i>
recovery	Nov-06	Dec-06	Nov-06	Nov-06	Dec-06	Nov-06	Nov-06	Nov-07
number of samples	3	9	3	3	3	3	3	3
MEMA ab.	301 $\pm$ 297	810 $\pm$ 623	239 $\pm$ 124	44 $\pm$ 29	184 $\pm$ 38	178 $\pm$ 128	66 $\pm$ 10	555 $\pm$ 176
ME ab.	247 $\pm$ 306	331 $\pm$ 607	23 $\pm$ 10	39 $\pm$ 29	77 $\pm$ 64	10 $\pm$ 9	32 $\pm$ 16	150 $\pm$ 192
MA ab.	12 $\pm$ 9	135 $\pm$ 186	80 $\pm$ 40	3 $\pm$ 1	69 $\pm$ 67	22 $\pm$ 16	33 $\pm$ 27	311 $\pm$ 17
MEMA S (obs.)	11 $\pm$ 2	13 $\pm$ 3	18 $\pm$ 3	12 $\pm$ 5	18 $\pm$ 6	14 $\pm$ 1	9 $\pm$ 3	17 $\pm$ 1
ME S (obs.)	4 $\pm$ 3	6 $\pm$ 2	9 $\pm$ 3	7 $\pm$ 3	9 $\pm$ 3	4 $\pm$ 2	4 $\pm$ 3	10 $\pm$ 1
MA S (obs.)	6 $\pm$ 3	7 $\pm$ 2	9 $\pm$ 2	5 $\pm$ 3	9 $\pm$ 4	10 $\pm$ 2	5 $\pm$ 1	7 $\pm$ 1
MEMA S(m300)	12 $\pm$ 6	10 $\pm$ 3	14 $\pm$ 1	15 $\pm$ 5	16 $\pm$ 6	9 $\pm$ 1	12 $\pm$ 5	15 $\pm$ 1
ME S(m300)	5 $\pm$ 4	8 $\pm$ 4	10 $\pm$ 3	8 $\pm$ 4	11 $\pm$ 3	5 $\pm$ 3	6 $\pm$ 6	14 $\pm$ 1
MA S(m300)	7 $\pm$ 1	6 $\pm$ 1	8 $\pm$ 1	7 $\pm$ 5	13 $\pm$ 8	6 $\pm$ 1	6 $\pm$ 1	6 $\pm$ 1
MEMA H'(loge)	0.9 $\pm$ 0.7	1.1 $\pm$ 0.3	1.7 $\pm$ 0.2	1.3 $\pm$ 0.6	1.6 $\pm$ 0.4	0.7 $\pm$ 0.0	1.3 $\pm$ 0.2	1.5 $\pm$ 0.2
ME H'(loge)	0.5 $\pm$ 0.8	1.0 $\pm$ 0.6	1.6 $\pm$ 0.2	0.9 $\pm$ 0.4	1.4 $\pm$ 0.4	0.8 $\pm$ 0.8	0.7 $\pm$ 0.4	1.6 $\pm$ 0.4

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MA H'(loge)	0.8 ± 0.6	0.9 ± 0.3	1.3 ± 0.3	1.3 ± 0.6	1.5 ± 0.2	0.5 ± 0.1	0.9 ± 0.5	0.7 ± 0.5
MEMA J'	0.3 ± 0.3	0.4 ± 0.1	0.6 ± 0.1	0.5 ± 0.2	0.6 ± 0.1	0.2 ± 0.0	0.6 ± 0.1	0.5 ± 0.1
ME J'	0.2 ± 0.4	0.5 ± 0.3	0.7 ± 0.0	0.5 ± 0.2	0.7 ± 0.2	0.5 ± 0.4	0.6 ± 0.3	0.7 ± 0.2
MA J'	0.5 ± 0.4	0.5 ± 0.2	0.6 ± 0.1	0.9 ± 0.0	0.7 ± 0.1	0.2 ± 0.0	0.6 ± 0.3	0.4 ± 0.3

983 Table A.2. Results of non-parametric Kruskal-Wallis tests (p values >0.05 are considered not significant: ns) on faunal abundance 64 cm⁻²
 984 (ab.), species richness (S), Shannon diversity (H'loge), Pielou's evenness (J'), and expected number of species S(m300) for the entire
 985 community (meio- and macrofauna: MEMA), the meiofauna (ME) and the macrofauna (MA). A: Controls on influence of sponge deployment
 986 length at vents (deployed 1 week, 1 month, 3 months long) and on basalt (deployed 1 week, 1 month long) B: Controls on suitability of sponges
 987 as settlement substrates: settlement substrates (s.s.) and *in situ* community collections at vents and on basalt were compared in 2006 and
 988 2007. C: Influence of time among settlement substrates at sites Tica, P-Vent, at all vent sites, and basalt in the years 2006, 2007, 2009 and
 989 pre-eruption 2001-2004. D: Comparison of vent and basalt communities from settlement substrates in the same year. E: Comparison of
 990 communities from settlement substrates between vent sites Tica, Sketchy, and P-Vent in 2006 and of Tica and P-Vent in 2007.
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	MEMA ab.	ME ab.	MA ab.	MEMA S	ME S	MA S	MEMA H'	ME H'	MA H'	MEMA J'	ME J'	MA J'	MEMA S(m300)	ME S(m300)	MA S(m300)
A: Control: deployment length															
Deployment. lenght vent	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Deployment length basalt	0.05	ns	0.05	ns	ns	ns	ns	ns	ns	ns	ns	0.05	ns	ns	ns
B: Control suitability settlement substrates															
In situ & s.s. vent 2006	ns	ns	ns	ns	ns	ns	0.04	ns	ns	ns	ns	ns	ns	ns	ns
In situ & s.s. basalt 2006	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
In situ & s.s. basalt 2007	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
C: Influence of time at single vent sites, at all vent sites, and on basalt															
Tica 2006, 07, 09	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Tica 2006, 07, 09, 2001/02	ns	ns	ns	0.03	0.06	0.02	ns	0.03	ns	ns	0.04	ns	ns	ns	ns
P-Vent 2006, 07	ns	0.05	0.05	0.04	ns	ns	ns	0.05	0.05	ns	0.05	ns	ns	ns	ns
Vent 2006, 07, 09	ns	ns	ns	0.002	0.04	0.002	ns	0.05	ns	ns	ns	ns	ns	0.05	0.01
Vent 2006, 07, 09, 2001/02	ns	ns	ns	0.001	0.006	0.001	ns	ns	0.006	ns	ns	ns	0.04	ns	0.001
Basalt 2006, 07, 09	ns	ns	ns	ns	ns	ns	ns	ns	0.04	ns	ns	ns	ns	ns	ns
Basalt 2006, 07, 09, 2003/04	ns	ns	ns	ns	0.03	ns	ns	ns	0.04	ns	ns	ns	ns	0.03	ns
D: Comparison of vent and basalt communities in the same year															
Vent & basalt 2006	0.02	ns	ns	ns	ns	ns	ns	ns	0.01	ns	ns	ns	ns	ns	ns
Vent & basalt 2007	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

Vent & basalt 2009	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	0.05	ns
Vent & basalt old	0.02	ns	0.01	ns	0.03	0.01	ns	ns	0.05	ns	ns	ns	0.01	0.01	ns
E: Comparison of vent sites in the same year															
Tica-Sketchy-P-Vent 2006	ns	0.03	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Tica-P-Vent 2007	ns	0.05	ns	0.03	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

993 Table A.3. Species occurrence pre- (from Gollner et al. 2010, Gollner et al. 2015) and post-eruption (this study). Species, size (ME =
 994 meiofauna; MA = macrofauna), and taxon (meiofauna: H – harpacticoid Copepoda, S – siphonostomatoid Copepoda, COP – other Copepoda,
 995 N – Nematoda, O – Ostracoda, A – Acari, F- Foraminifera; macrofauna: AN – Annelida, AR – Arthropoda, MO – Mollusca, CH – Chordata, EC
 996 – Echinodermata, CN – Cnidaria, NEM – Nemertini, PLAT - Platyhelminthes) are given. In addition, type of occurrence pre- and post-eruption is
 997 shown: AST (Axial Summit Trough): species occurred at vents and on basalt; BS (basalt specialist): species occurred only on basalt; VG (vent
 998 generalist): species occurred in at least two vent habitats; VS (vent specialist): species occurred only in a single vent habitat; T (tubeworm):
 999 species occurred at tubeworms post-eruption. Species presence is indicated by “1” for pre- and post-eruption.
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Species	size	taxon	TYPE-PRE- eruption	TYPE-POST- eruption	PRESENCE- PRE-eruption	PRESENCE- POST-eruption
<i>Amphisamytha galapagensis</i>	MA	AN	AST	AST	1	1
<i>Archinome roscea</i>	MA	AN	AST	AST	1	1
<i>Hesiospina vestimentifera</i>	MA	AN	AST	AST	1	1
<i>Lepidonotopodium williamse</i>	MA	AN	AST	AST	1	1
<i>Nereis sandersi</i>	MA	AN	AST	AST	1	1
<i>Ophryotrocha akessoni</i>	MA	AN	AST	AST	1	1
<i>Galapagomystides aristata</i>	MA	AN	AST	B S	1	1
<i>Nicomache arwidsoni</i>	MA	AN	AST	B S	1	1
<i>Paralvinella grasslei</i>	MA	AN	AST	T	1	1
<i>Glycera tessellata</i>	MA	AN	AST		1	
<i>Lepidonotopodium atalantae</i>	MA	AN	AST		1	
<i>Branchinotogluma</i> sp. 1	MA	AN	B S		1	
Flabelliderma	MA	AN	B S		1	
Syllidae	MA	AN	B S		1	
<i>Branchinotogluma sandersi</i>	MA	AN	V G	AST	1	1
<i>Branchinotogluma grasslei</i>	MA	AN	V G		1	
<i>Branchinotogluma hessleri</i>	MA	AN	V G		1	
<i>Branchiplicatus cupreus</i>	MA	AN	V G		1	
<i>Eulalia papillosa</i>	MA	AN	V G		1	

<i>Lepidonotopodium riftense</i>	MA	AN	V G		1	
<i>Levensteiniella plicata</i>	MA	AN	V G		1	
<i>Opisthotrochopodus alvinus</i>	MA	AN	V G		1	
<i>Paralvinella pandorae</i>	MA	AN	V S	AST	1	1
<i>Hesiolyra bergi</i>	MA	AN	V S		1	
<i>Polychaete sp.1</i>	MA	AN	V S		1	
<i>Prionospio sandersi</i>	MA	AN		B S		1
<i>Halice hesmonectes</i>	MA	AN		T		1
<i>Dahlella caldariensis</i>	MA	AR	AST	AST	1	1
<i>Ventiella sulfuris</i>	MA	AR	AST	AST	1	1
<i>Typhlotanais sp.1</i>	MA	AR	AST		1	
Amphipod sp. 4 - pre	MA	AR	B S		1	
<i>Alvinocaris lusca</i>	MA	AR	V G		1	
Amphipod sp. 1 - pre	MA	AR	V S		1	
Amphipod sp. 1 - post	MA	AR		B S		1
Amphipod sp. 4 - post	MA	AR		B S		1
Amphipod sp. 5 -post	MA	AR		B S		1
Tunicate	MA	CH	B S		1	
Anemone	MA	CN	V S		1	
Ophiura - pre	MA	EC	V G		1	
Ophiura - post	MA	EC		AST		1
<i>Lepetodrilus cristatus</i>	MA	MO	AST	AST	1	1
<i>Lepetodrilus elevatus</i>	MA	MO	AST	AST	1	1
<i>Lepetodrilus pustulosus</i>	MA	MO	AST	AST	1	1
<i>Gorgoleptis spiralis</i>	MA	MO	AST	B S	1	1
<i>Bythograea thermydron</i>	MA	MO	AST	T	1	1
<i>Lepetodrilus ovalis</i>	MA	MO	AST	T	1	1

<i>Rhynchopelta concentrica</i>	MA	MO	AST	T	1	1
<i>Bathymagarites symplector</i>	MA	MO	AST		1	
<i>Cyathermia naticoides</i>	MA	MO	V G	AST	1	1
<i>Eulepetopsis vitrea</i>	MA	MO	V G	AST	1	1
<i>Pachydermia laevis</i>	MA	MO	V G	T	1	1
<i>Levensteiniella kincaidi</i>	MA	MO	V G		1	
<i>Melanodrymia aurantiaca</i>	MA	MO	V G		1	
<i>Neomphalus fretterae</i>	MA	MO	V G		1	
<i>Nodopelta rigneae</i>	MA	MO	V G		1	
<i>Peltospira delicata</i>	MA	MO	V G		1	
<i>Peltospira operculata</i>	MA	MO	V G		1	
<i>Aplacophora</i> sp.1	MA	MO	V S		1	
<i>Lepetodrilus galriftensis</i>	MA	MO	V S		1	
<i>Provanna</i> cross hatch	MA	MO	V S		1	
<i>Provanna</i> riblet	MA	MO	V S		1	
<i>Clypeosectus delectus</i>	MA	MO		AST		1
<i>Ctenopelta porifera</i>	MA	MO		AST		1
<i>Lepetodrilus tevniatus</i>	MA	MO		AST		1
<i>Provanna</i> sp. 1	MA	MO		AST		1
<i>Solenogastres</i>	MA	MO		AST		1
<i>Gastropoda</i> sp. 2 (juv)	MA	MO		T		1
<i>Nemertea</i>	MA	NE	V S		1	
<i>Thermonemertes/Nemertini</i> sp.1	MA	NEM		AST		1
<i>Platyhelminthes</i> sp. 1	MA	PLAT		T		1
<i>Lohmannella</i> sp. 1	ME	A	V S		1	
<i>Copidognathus</i> sp. 1	ME	A		B S		1
<i>Barathricola rimensis</i>	ME	COP		AST		1

<i>Cheramyzon abyssale</i>	ME	COP		AST		1
<i>Cerviniopsis</i> sp. nov. 1	ME	COP		B S		1
<i>Abyssotherma pacifica</i>	ME	F	AST	AST	1	1
<i>Deuterammina</i> sp. 1	ME	F	AST		1	
Foraminifera sp. 4	ME	F	B S	B S	1	1
Foraminifera sp. 2	ME	F	B S		1	
Foraminifera sp. 3	ME	F	B S		1	
Forminifera sp. 1	ME	F	V S		1	
<i>Ameira</i> sp. 1	ME	H	AST	AST	1	1
<i>Amphiascus</i> sp.1	ME	H	AST	AST	1	1
<i>Halectinosoma</i> sp. 1	ME	H	AST	AST	1	1
<i>Xylora bathyalis</i>	ME	H	AST	AST	1	1
<i>Halophytophilus</i> sp.1	ME	H	AST		1	
<i>Mesochra</i> sp. 1	ME	H	B S	AST	1	1
<i>Ameiropsis</i> sp.1	ME	H	B S		1	
<i>Argestes</i> sp.1	ME	H	B S		1	
<i>Atergopedia</i> sp.1	ME	H	B S		1	
<i>Ectinosoma</i> sp. 1	ME	H	B S		1	
<i>Ectinosoma</i> sp. 2	ME	H	B S		1	
<i>Idomene</i> sp. 1	ME	H	B S		1	
<i>Idomene</i> sp. 2	ME	H	B S		1	
<i>Idomene</i> sp. 3	ME	H	B S		1	
<i>Leptotachidia</i> sp. 1	ME	H	B S		1	
<i>Sarsameira</i> sp. 1	ME	H	B S		1	
<i>Smacigastes barti</i>	ME	H	B S		1	
<i>Stenocopia</i> sp. 1	ME	H	B S		1	
<i>Stenocopia</i> sp. 2	ME	H	B S		1	

<i>Stenocopia</i> sp. 3	ME	H	B S		1	
<i>Bathylaophonte pacifica</i>	ME	H	V G	AST	1	1
<i>Ameira</i> sp. 2	ME	H	V S		1	
<i>Bradya</i> sp. 1	ME	H	V S		1	
Diosaccinae sp.1	ME	H	V S		1	
Harpacticoida sp. 1	ME	H	V S		1	
<i>Tetragoniceps</i> sp. 1	ME	H	V S		1	
<i>Bathylaophonte</i> sp. nov 1	ME	H		AST		1
Pseudotachiidae sp. 2	ME	H		AST		1
<i>Tisbe</i> sp. nov. 1	ME	H		AST		1
<i>Sarsameira</i> sp. 2	ME	H		B S		1
<i>Tisbe</i> sp. 2	ME	H		B S		1
<i>Halomonhystera hickeyi</i>	ME	N	AST	AST	1	1
<i>Thalassomonhystera fisheri</i>	ME	N	AST	AST	1	1
<i>Anticoma</i> sp.1	ME	N	AST		1	
<i>Chromadorita</i> sp.1	ME	N	AST		1	
<i>Leptolaimus</i> sp.1	ME	N	AST		1	
<i>Microilaimus</i> sp.1	ME	N	AST		1	
<i>Paralinhomoeus</i> sp.1	ME	N	AST		1	
<i>Neochromadora</i> aff. <i>poecilosoma</i>	ME	N	B S	AST	1	1
<i>Linhomoeus caudipapillosus</i> sp. n.	ME	N	B S	T	1	1
<i>Astomonema</i> sp. 1	ME	N	B S		1	
<i>Chromadora</i> sp. 1	ME	N	B S		1	
<i>Chromadorida</i> sp. 2	ME	N	B S		1	
<i>Euchromadora</i> sp. 1	ME	N	B S		1	
<i>Eurystomina</i> sp. 1	ME	N	B S		1	
<i>Metoncholaimus</i> sp. 1	ME	N	B S		1	

<i>Microloaimus</i> sp. 2	ME	N	B S		1	
<i>Monhysterida</i> sp. 2	ME	N	B S		1	
<i>Paracyatholaimus</i> sp. 1	ME	N	B S		1	
<i>Paracyatholaimus</i> sp. 2	ME	N	B S		1	
<i>Prooncholaimus</i> sp. 1	ME	N	B S		1	
<i>Rhabdocoma</i> sp. 1	ME	N	B S		1	
<i>Syringolaimus</i> sp. 1	ME	N	B S		1	
<i>Tripyloides</i> sp. 1	ME	N	B S		1	
<i>Daptonema</i> sp. 1	ME	N	V G		1	
<i>Halomonhystera</i> sp. 1	ME	N	V G		1	
<i>Paracanthochus</i> sp.1	ME	N	V S		1	
<i>Monhysteridae/Xylidae</i> sp. 1	ME	N		T		1
<i>Thomontocypris brightae</i>	ME	O	AST	AST	1	1
<i>Thomontocypris gollnerae</i>	ME	O	AST	AST	1	1
<i>Xylocythere vanharteni</i>	ME	O	AST	AST	1	1
<i>Prionotoleberis styx</i>	ME	O	AST		1	
<i>Polycopetta pax</i>	ME	O	V G		1	
<i>Ostracoda</i> sp. 2	ME	O		T		1
<i>Ostracoda</i> sp. 1	ME	O		T		1
<i>Aphotopontius limatulus</i>	ME	S	AST	AST	1	1
<i>Aphotopontius mammillatus</i>	ME	S	AST	AST	1	1
<i>Ecbathyron prolixicauda</i>	ME	S	AST	AST	1	1
<i>Scotoecetes introrsus</i>	ME	S	AST	AST	1	1
<i>Stygiopontius hispidulus</i>	ME	S	AST	AST	1	1
<i>Ceuthoecetes acanthothrix</i>	ME	S	AST	T	1	1
<i>Stygiopontius flexus</i>	ME	S	AST	T	1	1
<i>Aphotopontius probolus</i>	ME	S	AST		1	

<i>Ceuthocetes introversus</i>	ME	S	AST		1	
<i>Stygiopontius paxillifer</i>	ME	S	AST		1	
<i>Stygiopontius quadrispinosus</i>	ME	S	AST		1	
<i>Exrima</i> sp. 1	ME	S	B S		1	
<i>Aphotopontius acanthinus</i>	ME	S	V G	AST	1	1
<i>Aphotopontius arcuatus</i>	ME	S	V G	T	1	1
<i>Nilva torifera</i>	ME	S	V G	T	1	1
<i>Aphotopontius flexispina</i>	ME	S	V G		1	
<i>Ceuthoecetes aliger</i>	ME	S	V G		1	
<i>Rhogobius contractus</i>	ME	S	V G		1	
<i>Stygiopontius sentifer</i>	ME	S	V G		1	
<i>Stygiopontius stabilitus</i>	ME	S	V G		1	
<i>Benthoxynus tumidiseta</i>	ME	S	V S	AST	1	1
<i>Aphotopontius hydronauticus</i>	ME	S	V S		1	
<i>Stygiopontius mucroniferus</i>	ME	S	V S		1	

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